

## Cranial Growth in *Homo erectus*: How Credible Are the Ngandong Juveniles?

SUSAN C. ANTÓN\*  
Department of Anthropology, University of Florida,  
Gainesville, Florida 32611

**KEY WORDS** suture fusion; vault contours; cranial development; heterochrony

**ABSTRACT** Confusion exists regarding the developmental ages of numerous Asian and southeast Asian *Homo erectus* fossils because of Weidenreich's contention that *Pithecanthropus* fused its sutures prematurely relative to *H. sapiens*. I reevaluate the cranial developmental ages of the Ngandong "juveniles" (2, 5, 8, 9) based on a series of indicators of youth (superstructure development, suture development/fusion, and cranial thickness) and cranial contours. The Ngandong juveniles are compared with *H. sapiens* adults (n = 281) and subadults (n = 81) and with Ngandong and other *H. erectus* adults (n = 20) and subadults (n = 4). Cranial contours are assessed using bivariate plots of arc vs. chord measurements. All indicators suggest that Ngandong 5 and 9 are adults, whereas Ngandong 8 is an older juvenile or young adult and Ngandong 2 is a juvenile with a developmental age range of greater than 6 and less than 11 years. In addition, adult cranial contours and the pattern of contour development are similar between Ngandong adults and other *H. erectus* adults. There is nothing in the cranial contour data to suggest that Ngandong is, despite a relatively large brain, transitional in vault shape between *H. erectus* and *H. sapiens*. Am J Phys Anthropol 108:223–236, 1999.

© 1999 Wiley-Liss, Inc.

As *H. erectus* is the presumed ancestor to *Homo sapiens*, the developmental pattern of *H. erectus* should form the standard against which to assess the relative pedomorphy or peramorphy of our species (e.g., Antón, 1997a). However, in practice the African apes have often been used to infer ancestral growth trajectories in part because there are so few fossil juvenile hominids (Gould, 1977). To remedy this situation, we must be able to differentiate between adult and subadult fossils. We must be cautious and systematic in designating fossils as juvenile, both to maintain the veracity of developmental studies and to ensure that the more often studied adult samples include the full range of adult ages (e.g., Antón and Franzen, 1997).

Recent systematic analyses have developed explicit guidelines for distinguishing between subadults and young adults in the fossil record (Smith, 1993; Antón, 1997b; Antón and Franzen, 1997). However, Weidenreich (1943, 1951) recognized the vast majority of the purported juvenile *H. erectus* before these comparative samples and guidelines were known. He suggested what seem to be remarkably young developmental ages for a large number of the Asian/southeast Asian *H. erectus*, including Sangi-

Grant sponsor: University of Florida.

\*Correspondence to: Susan C. Antón, Dept. Anthropology, University of Florida, Gainesville, FL 32611.  
E-mail: anton@nervm.nerdc.ufl.edu

Received 19 August 1997; accepted 3 October 1998.

ran 3, Mojokerto, Ngandong<sup>1</sup> 2, 5, 8, 9, and Zhoukoudian Skull III, IV, VII, VIII, and IX (Koenigswald and Weidenreich, 1939; Weidenreich, 1943, 1951, unpublished). Upon systematic reevaluation, Weidenreich's ages for Mojokerto (18 months) and Sangiran 3 (8–9 years) have proven to be substantially too young; Mojokerto is between 4 and 6 developmental years (Antón, 1997b), and Sangiran 3 is an adult (Antón and Franzen, 1997).

These systematic differences reflect Weidenreich's (1941, 1943, 1951) contention that *Pithecanthropus* but not *Sinanthropus* fused its sutures rapidly, much as do the extant apes. He suggested that smaller brains induced earlier suture fusion. And on this basis he argued that vault form was linked with brain size and that fetalization was not a significant component of human evolution (Weidenreich, 1941). But this view also had practical consequences for hominid paleontology: for Weidenreich, any unfused suture relegated a specimen to subadult status.

Yet Weidenreich failed to make a compelling case that unfused sutures alone can gauge skeletal immaturity, especially when other indicators suggest skeletal maturity (Antón and Franzen, 1997). He reasoned that suture fusion must be the norm for adult *Pithecanthropus* because so many southeast Asian specimens have fused sutures. Thus, any unfused suture must indicate a subadult. However, acceptance of this argument creates fossil assemblages, such as those at Ngandong, that are nearly half juveniles, a taphonomically unlikely event. In addition, his hard evidence derives solely from Sangiran 4, in which moderate dental wear is associated with advanced suture fusion in the posterior vault. Significantly, Weidenreich did not find the same relationship in the more numerous *Sinanthropus* fossils. Nonetheless, and despite its lacking any anatomical connection between palate and vault, he felt that Sangiran 4 confirmed

the early fusion of sutures relative to dental wear (and age) in *Pithecanthropus*. Even if Sangiran 4 is not a chimera, dental wear rates vary so greatly with diet and paramasticatory activities that they instill little faith as measures of relative age between populations of unknown diet (e.g., Molnar, 1972; Molnar et al., 1983; Richards, 1984). Despite this tenuous evidence, Weidenreich's age designations for the Ngandong and Zhoukoudian specimens are used in the main sourcebook for paleoanthropological specimens, *The Catalogue of Fossil Hominids* (Oakley et al. 1975). And his age estimates have been supported in the most comprehensive recent study of the Ngandong fossils (Santa Luca, 1980).

Other recent studies are more variable in their treatment of the Weidenreich juveniles. As mentioned, the most comprehensive of these supports Weidenreich's age designations (Santa Luca, 1980). However, Wolpoff (1996) and Jacob (1967) explicitly consider all but Ngandong 2 to be adult. Wolpoff does not discuss his rationale, whereas Jacob uses suture fusion. Of other recent studies that include some Ngandong specimens but do not explicitly consider developmental age, some exclude (e.g., Lumley and Sonakia, 1985; Spiteri, 1985; Kennedy,<sup>2</sup> 1991; Leigh<sup>2</sup>, 1992; Bräuer and Mbua, 1992; Rightmire, 1993), whereas others include at least some of the purported juveniles (e.g., Gauld, 1996; Grimaud-Hervé, 1994; Grimaud-Hervé and Saban, 1996). Most studies of adults seem to exclude the Ngandong 2 frontal, while Ngandong 5 and 9 are more variably included. It is not always clear whether decisions to include/exclude Ngandong 5 and 9 are made because age is not an issue in the study or whether the specimens are considered juvenile, adult, or too fragmentary to include. Age is apparently not an issue in Grimaud-Hervé's inclusion of Ngandong 2, 5, and 9 in her studies of endocranial impressions since both adults and known subadults, including the Gibraltar and Teshik Tash juveniles, are sampled without comment (Grimaud-Hervé, 1994;

<sup>1</sup>Many authors use Ngandong and Solo specimen numbers interchangeably. However, specimen numbers do not translate directly between the two systems, and therefore caution is needed in comparing samples between studies. I use the numbering system of Oakley et al. (1975) and Santa Luca (1980), in which each specimen number is preceded by *Ngandong*. These numbers correlate with Weidenreich's (1951) Solo Skull numbers as follows: Ngandong 2 = Solo 2; Ngandong 5 = Solo 4; Ngandong 8 = Solo 7; Ngandong 9 = Solo 8.

<sup>2</sup>Neither Kennedy (1991) nor Leigh (1992) follows the numbering convention used here. They use Weidenreich's (1943) numbers but replace *Solo* with *Ngandong*. Thus, Ngandong V is Ngandong 6 of this study, and Ngandong IX is Ngandong 10 of this study. Neither include the Weidenreich juveniles.

TABLE 1. Distribution of cranial characters in Ngandong and other fossil hominids

Character <sup>1</sup>	<i>H. habilis</i>	<i>H. erectus</i>	Ngandong	Archaic <i>Hss</i> <sup>2</sup>	<i>Hss</i> <sup>2</sup>
Occipital torus	0	+	+	v	0
Keels/angular torus	0	+	+	v	0
Angulated occipital	0	+	+	v	0
Fissure between mastoid-tympanic	+	+	+	0	0
Sphenoid contributes to TMJ	0	v	v	v	+
Recess between entoglenoid-tympanic	0 <sup>3</sup>	+	+	v	v
Obelion depression	0	+	+	0	0
Postorbital constriction	s	s	w	v	w
Straight supraorbital	0	+	+	0	0
Supratral gutter	0	+	+	v	0
AP broad TMJ	0	+	+	v	++
Strong articular eminence	0	+	+	+	++
Weak postglenoid process	0	+	+	+	+
Anterior projecting supraorbital torus	0	+	+	v	0
Coincidenceinion and opisthocranion	0	+	+	v	0
Cranial capacity (cc) <sup>4</sup>	500–750	750–1,225	1,013–1,251	1,120–1,350	—

<sup>1</sup> First set of characters is synapomorphies for *H. erectus*.

<sup>2</sup> i, incipient; *Hss* is *Homo sapiens sapiens*; Symbols are s, strong; v, variable; w, weak; +, present; 0, absent; ++, very strong. Archaic *Hss* are Dali, Maba, Yunxian, Jinniushan, Kabwe, Ndutu. See text for other samples and trait definition.

<sup>3</sup> Tobias (1991) distinguishes the morphology of the medial glenoid fossa in *H. habilis* from that in *H. erectus* contra Bräuer and Mbua (1992).

<sup>4</sup> Cranial capacities are from Holloway (1981), Weidenreich (1943), and Howell (1994).

Grimaud-Hervé and Saban, 1996). However, Gauld (1996) implicitly considers Ngandong 5 and 9 but not Ngandong 2 adults. Alternatively, while age may be an issue, specimen completeness is explicitly the issue for Rightmire's (1993) exclusion of all the Ngandong juveniles. In contrast, the juvenile ages of Ngandong 5 and 9 do appear to be an issue for those studies that include even quite fragmentary adult remains; despite the fact that Ngandong 5 and 9 retain pertinent anatomical regions, both are excluded by Kennedy (1991), whereas Bräuer and Mbua (1992) exclude the more complete Ngandong 5. Antón and Franzen (1997) exclude both specimens explicitly because of their questionable ages. Given this disagreement in treatment and since the main published references of Ngandong consider these specimens subadults (Weidenreich, 1951; Oakley et al., 1975; Santa Luca, 1980), a full assessment of the skeletal maturity of the purported juveniles is needed to ensure the integrity of subadult and adult samples. Likewise, a clear understanding of the variation between and within fossil age classes requires the assessment of all specimens, not only the most complete or most remarkable.

The taxonomic status of the Ngandong hominids has been as confused as their developmental ages. The Ngandong hom-

inids are variously assigned to *H. erectus*, *H. soloensis*, and archaic *H. sapiens* (e.g., Weidenreich, 1951; Santa Luca, 1980; Rightmire, 1993; Wolpoff et al., 1994). Despite this disagreement, Table 1 demonstrates that Ngandong adults group with *H. erectus* on all cranial traits except mean brain size, for which their ranges overlap, and the correlated trait of postorbital constriction. This is true of traits considered either synapomorphic or autapomorphic for *H. erectus* by most researchers, such as cranial superstructures (metopic eminence, sagittal keel, and bregmatic eminence), occipital torus, and sharp angulation between the nuchal and squamous portions of the occipital (Delson et al., 1977; Santa Luca, 1980; Stringer, 1984; Andrews, 1984; Hublin, 1986; Kennedy, 1991; Li and Etler, 1992; Rightmire, 1993). It is also true of those characters considered synapomorphic by some (Andrews, 1984; Stringer, 1984; Li and Etler, 1992; Rightmire, 1993) but not all (Hublin, 1986; Kennedy, 1991; Bräuer and Mbua, 1992) researchers—characters such as a fissure separating the mastoid process from the tympanic plate (= mastoid fissure), lack of a sphenoid contribution to the glenoid fossa, and a recess between the entoglenoid pyramid and tympanic. And it is true of those characters that are either plesiomorphic or

of unclear polarity such as morphology of the temporomandibular joint, obelion depression, sagittal contours, postorbital constriction, and presence of a supratral gutter (Picq, 1990; Rightmire, 1993). Ngandong even groups with *H. erectus* based on those few characters that Wolpoff and colleagues (1994) accept as separating *H. erectus* and *H. sapiens*: anteriorly projecting supraorbital tori, thickening of the cranial wall involving both cortices and diplöe, strong angulation between occipital and nuchal planes, and coincidence of inion and opisthocranion.

Thus, in terms of shape characters that distinguish *H. erectus* vaults from other archaic and modern crania, Ngandong affiliates with *H. erectus* despite being chronologically younger than other *H. erectus*. While it remains possible that Ngandong represents its own species on the basis of cranial capacity and associated accommodations, its general bauplan and specific features are easily encompassed within the *H. erectus* morphospecies and in fact show remarkable continuity with the much older and smaller brained specimens from southeast Asia. For these reasons, I favor the inclusion of Ngandong in *H. erectus* with at most subspecific recognition (*sensu* Howell, 1994). Such an inclusion is consistent with recent comprehensive reviews of Ngandong (Santa Luca, 1980; Rightmire, 1993) and with implications of work in progress on aspects of the Ngandong cranial base (e.g., Durband, 1998; Robinson and Aiello, 1998). Although this argument is critical for the construction of the *H. erectus* hypodigm, the taxonomic status of Ngandong is not critical for determining the developmental age of the Ngandong juveniles since many of the comparisons used to determine developmental age are relative to modern human standards or to the Ngandong adults themselves.

Given the confusion regarding the developmental ages of the Ngandong juveniles (e.g., Santa Luca (1980) vs. Wolpoff [1996]) as well as the significance of *H. erectus* juveniles to questions of human heterochrony, I reevaluate the cranial developmental ages of the Ngandong juveniles using previously erected guidelines (Antón and Franzen, 1997). I focus here on the juveniles from Ngandong

because they are more complete than most of those from Zhoukoudian and because of Weidenreich's differing beliefs regarding the timing of sutural fusion in each group.

## MATERIALS AND METHODS

### Materials

Excavated in 1931–1933, the Ngandong hominids represent the largest single-locality sample of fossil hominids from island southeast Asia and the youngest *H. erectus* sample in the world. Just exactly how much younger the Ngandong remains are than those from China is still debated (see below). Openoorth and colleagues conducted controlled excavations of the 20 m "High Terrace" at Ngandong on the Solo River, Java, Indonesia, that yielded 25,000 vertebrate fossils and 12 hominid calvaria (Openoorth, 1932, 1937; Ter Haar, 1934). The Ngandong hominids were discovered throughout the course of the excavations, evenly distributed amongst the other fauna (Terra, 1943). Bovid teeth from Openoorth's excavations, the 1970s excavations by T. Jacob, and test excavations by C.C. Swisher yield dates of 27–53 kya based on destructive U-series and electron spin resonance techniques (Swisher et al., 1996). While it remains possible that the bovids and hominids are not associated, it is more parsimonious to consider them to be associated because of the similarity between the preservation of the hominids and fauna that indicates a low energy depositional environment, the lack of evidence of time transgression in the fauna, the large number of hominids that would have had to have been reworked, and the lack of source beds for such hominids (Swisher et al., 1996). Dates for the Ngandong 1 calvaria using a nondestructive gamma spectrometric U-series technique have been recently announced that are much older (>200 ky [Falguères et al., 1998; Yokoyama et al., 1998]) than the destructive U-series/ESR dates reported by Swisher and colleagues (1996). While this discrepancy continues an interesting debate regarding the age of Ngandong, it introduces a much more interesting debate regarding the dating techniques themselves. Because the gamma dates themselves are not yet published, this debate cannot be fully addressed here; however, the following



observations are possible. Both research groups agree that the Ngandong fauna and hominids are coeval (Sémah, personal communication), yet the dating methods present different ages. This would seem to indicate that there may be problems with one or the other technique. It is critical to note that, because of its nondestructive nature, the gamma-ray spectrometric technique not only requires some complicated three-dimensional modelling for the accurate detecting of the different isotopic ratios when nonflat specimens such as calvaria are used, but it also requires a small amount of destructive analysis to measure the  $^{234}\text{U}/^{238}\text{U}$  ratio accurately since the accurate determination of this ratio by gamma-ray counting is not possible due to interference from other gamma rays, without introducing known or "correct" intensities (Simpson and Grün, in press). If different values for these intensities are used, as in previous work by Yokoyama, then the true value of the  $^{234}\text{U}/^{238}\text{U}$  ratio will be lower and the age will be similarly increased (see Simpson and Grün, in press). Yet no destructive analyses were conducted to produce the age of the Ngandong 1 calvaria (Falguères, personal communication). Given the data currently at hand, the alpha spectrometric U-series and ESR techniques appear to be more reliable than the completely nondestructive gamma spectrometric technique used by Falguères et al. (1998). However, clearly more work is required to resolve the geologic age of the Ngandong hominids. This work must include the evaluation of the reliability of both nondestructive gamma-ray spectrometric and destructive alpha spectrometric U-series/ESR dates against an accepted radiometric standard such as argon-argon. Surprisingly, this work has not been done for either technique.

Regardless of their geologic age, it is their morphology alone that should dictate the taxonomic status of the Ngandong hominids. Of the purported Ngandong juveniles (Ngandong 2, 5, 8, 9), only Ngandong 9 was recognized as a hominid at the time of its discovery. For this reason Von Koenigswald, rather than the other workers, removed Ngandong 9 in 1933 (Weidenreich, 1951).



Fig. 1. Anterior view of Ngandong 2. Superior is toward top of page. Note metopic keel and absence of any significant supratatorial development. For scale, glabella-bregma chord is 105 mm. Photo by Bierwert-Logan (1947), courtesy Department of Library Services, American Museum of Natural History, negative 125383.

The Ngandong juveniles represent various cranial elements. Ngandong 2 (Solo 2) is an isolated frontal missing the anterior lateral portion on the right side (Fig. 1). Midline structures including the glabellar region are intact. The specimen is composed of several pieces reconstructed with a brown-colored adhesive and coated with a glossy substance, perhaps preservative. None of the conjoins appear to have distorted the original morphology, except for the fragment comprising the right inferior coronal suture. This piece is angled slightly medially, resulting in a slightly narrower frontal breadth in this region. A metopic keel and incipient bregmatic eminence are present. Ngandong 5 (Solo 4) consists of a frontal and of left and right parietals reconstructed from multiple fragments with a brown adhesive and coated with a glossy material (Fig. 2). No evident distortion was introduced by the reconstruction, although the glossy material obscures some details of microstructure. A bregmatic eminence, metopic keel, and angular torus are present. A large section of the ectocranial surface of the right posterior parietal shows evidence of bone loss and sclerotic bone formation attributed to antemortem

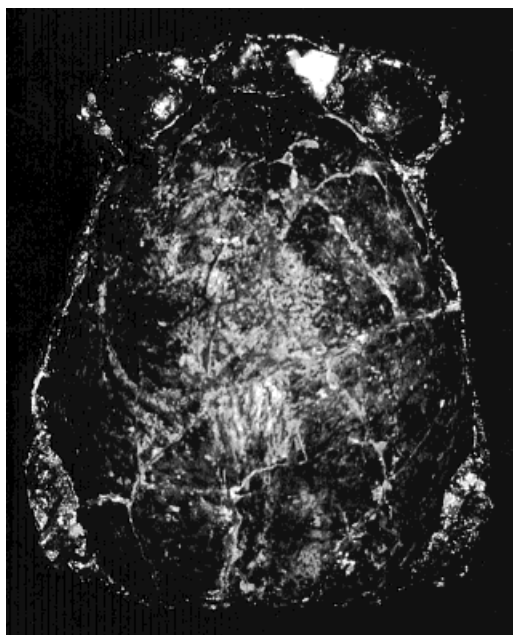


Fig. 2. Endocranial view of Ngandong 5. Note fused coronal suture and thickness of parietomastoid suture. For scale, biasterionic breadth is approximately 127 mm.



Fig. 3. Endocranial view of Ngandong 8. Superior is toward top of page.

trauma by Weidenreich (1951). Ngandong 8 (Solo 7) is a fragment of the right posterior inferior parietal at asterion (Fig. 3). Portions of the right lambdoidal, parietomastoid, and squamosal sutures are preserved and patent. Endocranially, the sigmoid sulcus is preserved, as are two vascular channels for posterior branches of the middle



Fig. 4. Superior view of Ngandong 9. Note adhesive at sagittal suture and extreme surface weathering. Anterior is toward top of page. For scale, bregma-lambda chord is 104 mm.

meningeal artery. Ngandong 8 is also coated with the glossy substance. An incipient angular torus is present. Ngandong 9 (Solo 8) consists of largely complete left and right parietals joined in the region of the sagittal suture by a mass of brown adhesive (Fig. 4). The outer table is weathered and cracked, and the glossy material is not as thick as on Ngandong 5. The coronal and lambdoidal sutures are largely intact and patent, although the parietals are broken posterior to the coronal suture site in some places. Angular tori are present.

Ngandong 2 has been estimated to be between 3 and 7 years of age (Openoorth, 1937; Weidenreich, 1951; Oakley et al., 1975). Ngandong 5, 8, and 9 have not been assigned developmental ages but were simply considered adolescents (Weidenreich, 1951; Oakley et al., 1975; Santa Luca, 1980). On the basis of cranial thickness, Weidenreich (1951) considered Ngandong 8 the youngest and Ngandong 9 the oldest of the adolescents, whereas Santa Luca (1980) considers Ngandong 5 the oldest adolescent on the basis of suture fusion.

I compare the Ngandong juveniles morphologically and metrically with the Ngandong

TABLE 2. Sample sizes and sources of hominid cranial material

Sample	Adult N	Subadult N	Origin of metrics <sup>1</sup>
<i>Homo sapiens</i>			
Unaffiliated	—	51	Antón, UOP
Modern Caucasian	9	—	Antón, UF
Britain—Spitalfields	20	20	Antón, BMNH
Papua New Guinea	89	—	Hambly, 1940
Australia	123	10	Antón, BM/AMNH
Fossil <i>Homo sapiens sapiens</i> (Coobol Creek, Kow Swamp 1, 5, 7, 8; Nacurrie, 1, 2; Keilor; Wajak 1)	41	—	Antón; Brown, 1989; Jacob, 1967
<i>Homo erectus</i>			
Ngandong <sup>2</sup> 2, 5, 8, 9	—	4?	Antón
Mojokerto, KNM-WT 15000, Zhoukoudian III, VIII	—	4	Antón
Sangiran 2, 3, 4	3	—	Antón
OH-9, KNM-ER 3733, 3883, Sangiran 10, 12, 17	6	—	Wood, 1991
Ngandong <sup>2</sup> 1, 3, 6, 10, 11, 12; Trinil, Zhoukoudian II, X, XI, XII	11	—	Santa Luca, 1980

<sup>1</sup> Comparisons made by Antón on original and cast material as noted in text. AMNH, American Museum of Natural History; BMNH, Natural History Museum, London; UF, University of Florida; UOP, University of the Pacific. Other abbreviations as per text.

<sup>2</sup> See footnote one regarding numbering conventions of Ngandong hominids.

adults and with adults and subadults of other *H. erectus* and *H. sapiens*. I used original specimens and casts of Mojokerto, Ngandong 2, 5, 8, 9, Sangiran 2, 3, 4, 12, 17, and Trinil and casts only of other fossil hominids (Table 2). Metrics were taken by me or from the literature as per Table 2. The more complete *H. erectus* subadults used here are, from developmentally oldest to youngest, Skull III, KNM-WT 15000, and Mojokerto. Zhoukoudian Skull III is either an older juvenile (Black, 1931) or a young adult that clusters with *H. erectus* subadults on frontal but not occipital contours (Antón, 1997b). Such patterning may entail regional morphological differentiation in vault shape, the analysis of which is beyond the scope of the present study. Zhoukoudian Skull III is viewed here as an older adolescent or young adult.

### Methods

For each Ngandong juvenile I evaluated indicators of youth, including vault thickness, superstructure development, sutural development, and sagittal vault contours. Three aspects of cranial vault thickness should distinguish young adult from subadult *H. erectus*: 1) three layers of fully differentiated cranial bone, 2) fully developed, localized outer table hypertrophy of all cranial superstructures, including eminences, keels, and tori, and 3) values of absolute vault thickness within adult

*H. erectus* ranges (Antón and Franzen, 1997) (Table 3). A specimen is considered an adult for thickness if cranial thickness is within the adult range and the pattern of thickness throughout that vault is consistent with that exhibited by known adults. For example, a specimen should not have both the thickest occipital torus and the thinnest supraorbital torus of adult specimens. Although each of these features develops along a continuum, the full development of each, considered in conjunction with other indicators as described below, provides multiple avenues for assessing skeletal maturity.

The cranial superstructures (metopic and bregmatic eminences, sagittal keel, and occipital and angular tori) are localized thickenings of ectocranial bone and diplöe in adult *H. erectus* (Weidenreich, 1940; Hublin, 1978, 1986) that develop as the cranial tables differentiate throughout childhood and adolescence. The relative development of cranial superstructures in the Ngandong juveniles is compared with the pattern and development in other subadult *H. erectus*. Based on the Mojokerto specimen, the occipital torus and metopic eminence develop before the bregmatic eminence, sagittal keel, and angular torus (Antón, 1997b). The occipital torus is more developed than the metopic keel in Mojokerto, suggesting that the occipital torus is the first of the superstructures to differentiate. The order of acquisition amongst the other three characters is not

TABLE 3. Cranial measurements (in millimeters)

	Ngandong 2	Ngandong 5	Ngandong 8	Ngandong 9	Ngandong adults <sup>3</sup> range	<i>H. erectus</i> adults <sup>3</sup> x (sd)	<i>H. erectus</i> adults <sup>3</sup> range
Thickness at							
Bregma	7.2	8.0	—	10.0	8.0–11.0	8.3 (1.2)	—
Asterion	—	(15.4) <sup>1</sup>	9.7	(17.3) <sup>1</sup>	—	11.3 (2.9)	—
Parietal Eminence	—	—	—	13.5	7.9–11.8	13.3 (1.4)	—
Length							
Frontal arc	117.0	119.0 <sup>2</sup>	—	—	107–120	—	90–128
Frontal chord	105.0	113.7	—	—	103–116	—	88–120
Parietal arc	—	104.0	—	111.0	101–115	—	86–115
Parietal chord	—	98.5	—	103.6	96–109	—	82–109

<sup>1</sup> Thickness of parietal (angular torus) superior to asterion. These values are larger than those taken at asterion would be.

<sup>2</sup> Bregma position estimated due to suture fusion.

<sup>3</sup> Ngandong adult ranges from Gauld (1996); her midparietal measure is located slightly differently than and gives smaller values than the parietal eminence as measured here or by Brown (1994); *H. erectus* mean vault thickness values from Brown (1994). Length ranges are for adults in this study. Individual thickness and length measurements are by Antón (this study).

discernible from the juveniles available. I also evaluate development of cranial superstructures by comparing vault thickness at bregma, asterion, and parietal eminence with ranges for adults from Ngandong and other adult *H. erectus* (after Brown, 1994; Gauld, 1996). Incipient rather than full development of cranial superstructures is considered a strong indicator of subadult status.

I examined the development of sutural interdigitation by comparing development of the sutural face (sensu Antón and Franzen, 1997), ectocranial sutural complexity (sensu Martin, 1914), and bony sutural fusion (sensu Meindl and Lovejoy, 1985) in the Ngandong specimens with adult and adolescent *H. sapiens* and *H. erectus*. Although the age of bony sutural fusion is notoriously variable in humans, endo- and ectocranial vault suture fusion is rarely encountered during adolescence in nonpathological individuals (Meindl and Lovejoy, 1985; Cohen, 1986; Buikstra and Ubelaker, 1994).

*H. erectus* sagittal vault contours change with growth of the face and cranial superstructures; frontal and parietal contours flatten and occipital contours become more angulated (Antón, 1997a,b; Antón and Franzen, 1997; Antón and Leigh, 1998). The plots are constructed using a mixed-sex sample, and there is no indication that there are differences in vault contours between the sexes (sex inferred from robusticity). As in previous studies, I used log-log plots of arc vs. chord measurements to determine whether vault curvatures of Ngandong 2, 5, and 9

show similar patterns relative to adults from Ngandong that *H. erectus* juveniles show to *H. erectus* adults and, if so, whether the Ngandong juveniles associate with *H. erectus* subadults or adults (Figs. 5, 6). Log plots are considered the most appropriate when considering allometric relationships. Arcs were taken in the sagittal plane with a steel tape placed along the ectocranial surface of each frontal (glabella to bregma) and parietal (bregma to lambda). Chords were straight-line distances between the same points using Mitutoyo digital sliding calipers. Least-squares regressions were calculated by groups using Systat, version 5.0 (Evanston, IL). A least-squares model is considered appropriate because there is a priori reason to designate chord measurements as the independent (X) variable as the indicator of size to which the arc lengths (Y) are related. Nonetheless, given the wide confidence intervals, it is unlikely that significant differences would be obtained using different bivariate techniques, and indeed there are not important differences when using reduced major axis techniques (see Antón and Weinstein, in press). Tsutakawa and Hewett's (1977) quick test was used to assess elevation of data points above the regression line, or essentially differences in y-intercept values between two groups with the same slope (Table 4). *P* values less than 0.01 were considered significant.

In the final assignment of cranial developmental age, it is important to consider sexual dimorphism. Since the male skull is usually thought to be both larger and more robust



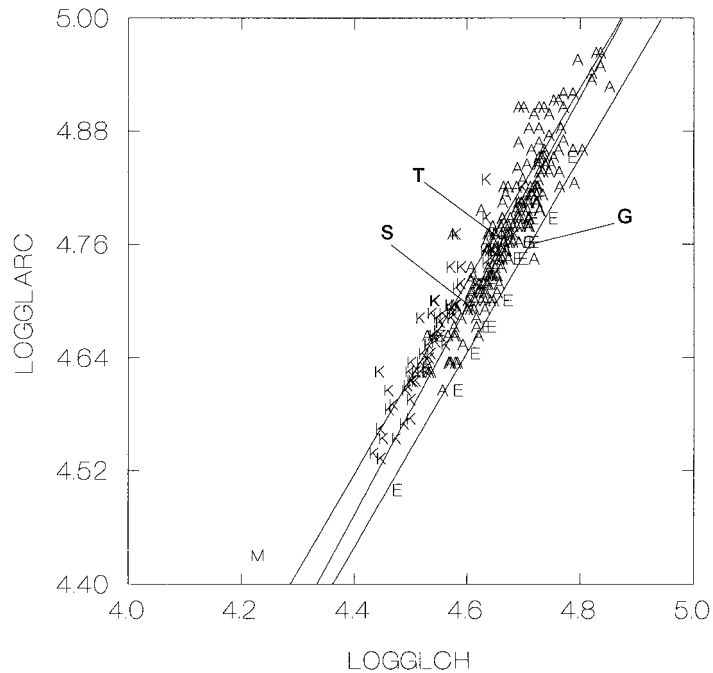


Fig. 5. Log-log plots of frontal arc (logglarc) vs. chord (logglch) lengths. A, adult *H. sapiens*; E, adult *H. erectus* including Ngandong adults; G, Ngandong 5; K, juvenile *H. sapiens*; M, Mojokerto; S, Skull III; T, Ngandong 2. All Ngandong adults are Es visible on or below the *H. erectus* regression line. Regression lines from left to right are least-squares regressions for *H. sapiens* juveniles, *H. sapiens* adults, and *H. erectus* adults.

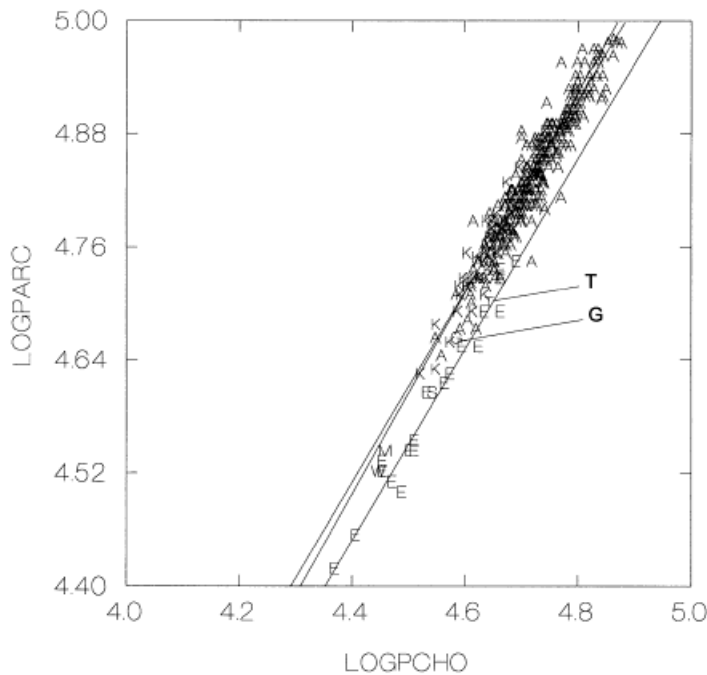


Fig. 6. Log-log plots of parietal arc (logparc) vs. chord (logpcho) lengths. A, adult *H. sapiens*; E, adult *H. erectus* including Ngandong adults; G, Ngandong 5; K, juvenile *H. sapiens*; M, Mojokerto; S, Skull III; T, Ngandong 9; W, KNM-WT 15000. Regression lines from left to right are least-squares regressions for *H. sapiens* juveniles, *H. sapiens* adults, and *H. erectus* adults. Es between M and W are KNM-ER 3883 and Zhoukoudian Skull XI.

than the female, it may be possible to confuse a juvenile male for an adult female. The reverse, confusing an adult (small) female for a juvenile, is less likely, as the lines of

evidence used do not resort solely to metric features but to relative development of structures. It is in the assessment of questionable cases that the use of multiple lines of evi-

TABLE 4. Least squares regression statistics and significance tests for differences between y-intercepts<sup>1</sup>

	n	Slope	y-intercept	Standard error	R <sup>2</sup>	<i>H. erectus</i> vs. <i>H. sapiens</i> (y-intercept)
Frontal arc vs. frontal chord (independent)						
Adult <i>H. erectus</i> (without ?juveniles)	16	1.03	-0.09	0.08	0.92	Smaller
Adult <i>H. sapiens sapiens</i>	190	1.10	-0.36	0.03	0.84	—
Juvenile <i>H. sapiens sapiens</i>	67	0.99	0.16	0.02	0.98	—
Parietal arc vs. parietal chord (independent)						
Adult <i>H. erectus</i> (without ?juveniles)	19	1.01	0.03	0.04	0.97	ns
Adult <i>H. sapiens sapiens</i>	281	1.01	0.05	0.02	0.89	—
Juvenile <i>H. sapiens sapiens</i>	66	0.94	0.38	0.02	0.97	—

<sup>1</sup> ns, not significant,  $P > 0.01$ ; smaller,  $P < 0.01$  and *H. erectus* smaller than *H. sapiens sapiens*. Differences between these values and Antón (1997b) relate to larger sample sizes here and exclusion of Ngandong 5 and 9 from adult *H. erectus* sample.

dence is critical. The relative consistency of results among and within lines of evidence is particularly important. A specimen is considered to be in an age category that is certain (i.e., adult or subadult) if all lines of evidence indicate that age status and if there is no internal inconsistency within any of these lines, such as cranial thickness or superstructure development. However, a specimen that exhibits inconsistency among the different lines of evidence or within any given line, such as cranial thickness, is assigned to the transitional category of older subadult/young adult. It should be noted that we are evaluating cranial developmental age (sensu Antón, 1997b), the variable of interest in this case being whether a particular cranium had achieved maturity—finished skeletal growth—prior to the individual's death. Cranial developmental maturity may or may not correlate with reproductive maturity and may be achieved at different ages in males and females (Bogin, 1994). However, the assessment of cranial developmental maturity is important to fossil studies, as it allows comparison among fully grown forms of each taxon and excludes those specimens which, for reasons of incomplete growth, have a different morphotype.

## RESULTS

### Cranial thickness, sutures, and superstructures

Cranial thickness, sutural, and superstructure development suggest that Ngandong 5 and 9 are adults, whereas Ngandong 8 is an older subadult or young adult, and Ngandong 2 is a subadult between 6 and 11 developmental years.

Cranial thickness and superstructure development in Ngandong 5 and 9 are within the range of adults from Ngandong and other adult *H. erectus* (Table 3). The presence of fully developed cranial superstructures such as the bregmatic eminence (Ngandong 5) and angular torus (Ngandong 5 and 9) also indicates full development of all three layers of cranial bone. The presence of fully developed angular tori in both specimens strongly suggests they are adults since *H. erectus* juveniles develop an occipital torus, metopic keel, and probably a bregmatic eminence before the sagittal keel or angular torus (Antón, 1997b).

Where visible, sutural faces of Ngandong 5 and 9 are as interdigitated as other adult *H. erectus*, or they are fused. None of the sutures visible in Ngandong 9 (coronal, lambdoidal, parietomastoid) or Ngandong 5 (parietomastoid, lambdoidal) exhibit the transitional form of interdigitation typical of human children's crania (Martin, 1914). On the contrary, the coronal suture of Ngandong 9 exhibits a full series of interlocking extensions more developed than Ngandong 2 and comparable to those seen in modern *H. sapiens* with third molars in occlusion (see Antón and Franzen, 1997). The pars bregmatica and pars complicata of the coronal suture are fully differentiated in Ngandong 9 (sensu Martin, 1914). The coronal suture and portions of the sagittal suture are fused endo- and ectocranially in Ngandong 5. This fusion is not pathological; there is no indication of abnormal vault shape or size or increased intracranial pressure based on endocranial impressions that would indicate that this fusion was either congenitally or

traumatically induced (for bony indicators see Cohen, 1986; Richards and Antón, 1991; Pederson and Antón, 1998). This fusion may indicate that Ngandong 5 is the older of the two adults, as no definitive sutural fusion is present in Ngandong 9. However, the fact that the parietal is often broken posterior to the coronal suture site rather than cleanly separated along the suture face may suggest that the coronal suture of Ngandong 9 was partially obliterated. In addition, suture fusion sequences and ages are highly variable among individual *H. sapiens* (Buikstra and Ubelaker, 1994), suggesting that suture fusion in Ngandong 5 does not necessarily indicate an older age than Ngandong 9.

Ngandong 8 is slightly less thick than adult *H. erectus* at asterion, although three tables of bone are clearly differentiated (Table 3). The angular torus is only partially expressed. However, because the angular torus develops later than other superstructures and because the specimen is fragmentary, classification as an older subadult/young adult is warranted. Classification as an older subadult/young adult is warranted since the question of whether Ngandong 8 was a large subadult (perhaps male) or small adult (perhaps female) cannot be resolved without information from portions of the cranium not preserved in this specimen.

Ngandong 2 is much thinner than adults from Ngandong, other adult *H. erectus*, and Ngandong 5. However, diploë formation is evident from the incipient bregmatic eminence (Table 3). The coronal suture face is less interdigitated and thinner than in young adult *H. erectus* or Ngandong 9. In addition, the coronal suture is thickened mostly at bregma, not laterally. Juvenile human crania thicken earliest at bregma and later at the lateral extensions of the suture, whereas adult sutures are thickened both at bregma and more laterally (Antón and Franzen, 1997). The metopic keel and bregmatic eminence, although incompletely expressed in Ngandong 2, are better developed than those of Mojokerto. The supraorbital torus region exhibits anterior enlargement only around glabella; lateral structures are undeveloped. Although better developed than in Mojokerto, the supraorbital torus itself is not a discrete structure nor as large as that in

KNM-WT 15000 or Skull III. Overall, Ngandong 2 is absolutely larger than Mojokerto but significantly smaller than both KNM-WT 15000 and Skull III.

### Cranial contours

Cranial vault contours also suggest that Ngandong 5 and 9 are adults, whereas Ngandong 2 is a subadult (Table 3; Figs. 5, 6). Frontal contours are flatter in adult *H. erectus* (and Ngandong adults) than in adult *H. sapiens* or subadult *H. erectus* (Antón, 1997b; this study); slopes do not differ between adults of the two species, but the regression line for *H. erectus* adults is transposed significantly below that of adult and subadult *H. sapiens* (Table 4). The Ngandong 5 frontal plots with adult *H. erectus* including Ngandong adults, whereas Ngandong 2 plots with *H. sapiens*, indicating its subadult status. Parietal contour slopes and intercepts do not differ significantly between adults of the two species; however, subadult *H. erectus* are more rounded in contour than adults. Ngandong 5 and 9 plot with adult *H. erectus* (and Ngandong adults) for parietal contours.

### DISCUSSION

All indicators suggest that Ngandong 5 and 9 are adults, that Ngandong 8 is a younger adult or older subadult, and that Ngandong 2 is a subadult. Based on relative suture fusion, Ngandong 5 may be the older of the two adults, although this remains uncertain. These results differ from Weidenreich (1951) and Santa Luca (1980), both of whom argue that Ngandong 5, 8, and 9 are adolescents.

Developmental indicators and overall size suggest that the Ngandong 2 frontal is from a slightly older subadult than the Mojokerto specimen but is younger than KNM-WT 15000 or Skull III specimens. Such a placement provides a developmental age range of greater than 6 and less than 11 years, based on modern human subadult standards (ages after Antón, 1997b; Smith, 1993). That is, Ngandong 2 died during the early part of its later childhood years (*sensu* Bogin, 1988), sometime after the eruption of its first permanent tooth but before complete eruption of its permanent dentition. Based

on KNM-WT 15000, by near the end of this time the supraorbital torus region is substantially developed in *H. erectus*. Such development may be linked both to growth of the face and the cranial base. The nearly complete lack of supraorbital torus development in Ngandong 2, compared with that in KNM-WT 15000 and Skull III, suggests that Ngandong 2 is at the younger end of this projected age range.

The subadult sample of *H. erectus* now includes, from youngest to oldest, Mojokerto, Ngandong 2/Skull VIII, and KNM-WT 15000. The older subadult or young adult category includes Ngandong 8 and Skull III and IX (an article by Antón currently in press has information on Zhoukoudian specimens). Four of these specimens are complete enough to include in allometric analyses of cranial growth in *H. erectus*. Such analyses of cranial contours indicate different ontogenetic patterns in *H. erectus* and *H. sapiens* (Antón, 1997a,b; Antón and Leigh, 1998).

Adult cranial contours and the pattern of contour development are similar between Ngandong and other *H. erectus* samples. All Ngandong adults have flatter frontals and parietals than modern humans but similar shapes as other adult *H. erectus*. Ngandong 2, a subadult according to the cranial indicators of youth, has a more rounded frontal than its adult counterparts, including Ngandong 5 and 9. A similar pattern is seen between Mojokerto and Skull III frontals and adult *H. erectus* (Antón, 1997b). However, this change in vault contours between subadults and adults is not present in *H. sapiens* (Antón and Leigh, 1998). In fact, adult *H. sapiens* vault contours are more like subadult *H. erectus* contours. *H. sapiens* is in this respect pedomorphic relative to *H. erectus*.

Nothing in the cranial contour data suggests that Ngandong is in any way transitional between *H. erectus* and *H. sapiens*. Although Archaic *H. sapiens* may have similar contours to *H. erectus* and thus Ngandong, this does not diminish the fact that Ngandong does not plot intermediately between *H. erectus* and recent *H. sapiens*. Despite relatively large brains compared with other *H. erectus*, adult Ngandong frontals and parietals are not positioned halfway

between adult *H. erectus* and modern humans (Figs. 5, 6). This finding is particularly significant because I compare Ngandong with fossil and recent Australian crania, the modern humans relative to whom Ngandong is often considered transitional (Weidenreich, 1946; Thorne and Wolpoff, 1981; Wolpoff, 1996). This dissociation between vault shape and cranial capacity suggests that absolute brain size may not be a good taxonomic Rubicon.

Despite a number of references suggesting that the Ngandong juveniles are mostly adults (Openoorth, 1937; Jacob, 1967; Wolpoff, 1996), Weidenreich's age designations have been widely accepted (e.g., Oakley et al., 1975; Santa Luca, 1980). As a result, Ngandong 5 and 9 are often excluded from studies of adult *H. erectus* (e.g., Kennedy, 1991; Leigh, 1992) and even from those that consider fragmentary remains (Santa Luca, 1980; Bräuer and Mbua, 1992; Antón and Franzen, 1997). Ironically, the impact of Weidenreich's age designations has had a longer lasting if less acknowledged effect on hominid paleontology than the argument against fetalization in human evolution that they were used to support.

#### ACKNOWLEDGMENTS

I am grateful to the following individuals for access to specimens/documents in their care: Dr. T. Jacob, Gadjah Mada University, Yogyakarta, Indonesia; Dr. F. Aziz, Quaternary Research Lab, Geological Research and Development Center, Bandung, Indonesia; Dr. J.L. Franzen, Senckenberg Museum, Frankfurt; Dr. J. de Vos, P. Storm and R. van Zelst, Rijksmuseum, Leiden; Dr. C. Stringer, T. Molleson, and R. Kruszynski, Natural History Museum, London; Drs. F.C. Howell and T.D. White, Laboratory for Human Evolutionary Studies, UCB; Dr. I. Tattersall, J. Grand, G. Sawyer, V. Wheat, and T. Baione, AMNH; Dr. D. Dechant, Atkinson Collection, University of the Pacific, School of Dentistry; and Dr. W. Maples, C.A. Pound Human Identification Laboratory, UF. Drs. T. Jacob, S.R. Leigh, W.R. Leonard, C.C. Swisher III, and the reviewers provided helpful discussion.



## LITERATURE CITED

- Andrews P. 1984. On the characters that define *Homo erectus*. *Courier Forschungsinstitut Senckenberg* 69: 167–175.
- Antón SC. 1997a. Cranial growth in *Homo erectus*: the development of frontal recession and occipital angulation. *Am J Phys Anthropol Suppl* 24:67 (abstract).
- Antón SC. 1997b. Developmental age and taxonomic affinity of the Mojokerto child, Java, Indonesia. *Am J Phys Anthropol* 102:497–514.
- Antón SC, Franzen JL. 1997. The occipital torus and developmental age of Sangiran-3. *J Hum Evol* 33:599–610.
- Antón SC, Leigh SR. 1998. Paedomorphosis and neoteny in human evolution. *J Hum Evol* 34:A2 (abstract).
- Antón SC, Weinstein KJ. in press. Artificial deformation in fossil Australians revisited. *J Hum Evol*.
- Black D. 1931. On an adolescent skull of *Sinanthropus pekinensis* in comparison with an adult skull of the same species and with other hominid skulls, recent and fossil. *Palaeontol Sin Series D* 7(2):1–114.
- Bogin B. 1988. Patterns of human growth. New York, Cambridge University Press.
- Bogin B. 1994. Adolescence in evolutionary perspective. *Acta Paediatr Scand Suppl* 406:29–35.
- Bräuer G, Mbua E. 1992. *Homo erectus* features used in cladistics and their variability in Asian and African hominids. *J Hum Evol* 22:79–108.
- Brown P. 1989. Coobool Creek: a morphological and metrical analysis of the crania, mandibles and dentitions of a prehistoric Australian human population. *Terra Australis* 13. Canberra: Australian Natl Univ.
- Brown P. 1994. Cranial vault thickness in Asian *Homo erectus* and *Homo sapiens*. In Franzen JL, editor. 100 years of *Pithecanthropus*: the *Homo erectus* problem. *Courier Forschungsinstitut Senckenberg* 171:33–46.
- Buikstra JE, Ubelaker DH. 1994. Standards for data collection from human skeletal remains. *Arkansas Archeological Survey Research Series* 44. Fayetteville: Arkansas Archeolog Survey.
- Cohen MM Jr. 1986. Craniosynostosis: diagnosis, evaluation and management. New York: Raven Press.
- Delson E, Eldridge N, Tattersall I. 1977. Reconstruction of hominid phylogeny: a testable framework based on cladistic analysis. *J Hum Evol* 6:263–278.
- Durband AC. 1998. The cranial base of the Ngandong hominids: implications for modern human origins. *Am J Phys Anthropol Suppl* 26:79 (abstract).
- Falguères C, Saleki H, Sémah F, Yokoyama Y, Féraud G, Fontugne M. 1998. Recentes datations de sites préhistoriques à Java. Abstracts of Origine des peuplements et chronologie des cultures paléolithiques dans le sud-est Asiatique 1998:38 (abstract).
- Gauld SC. 1996. Allometric patterns of cranial bone thickness in fossil hominids. *Am J Phys Anthropol* 100:411–426.
- Gould SJ. 1977. Ontogeny and phylogeny. Cambridge: Harvard University Press.
- Grimaud-Hervé D. 1994. Evolution of the Javanese fossil hominid brain. In: Franzen JL, editor. 100 years of *Pithecanthropus*: the *Homo erectus* problem. *Courier Forschungsinstitut Senckenberg* 171:61–68.
- Grimaud-Hervé D, Saban R. 1996. Les empreintes vasculaires observées sur les moulages endocraniens d'hominides fossiles et actuels. *Anthropologie* 34: 27–34.
- Hambly WD. 1940. Craniometry of New Guinea. *Field Museum of Natural History, Anthropological Series*, 25:83–290.
- Holloway RL. 1981. The Indonesian *Homo erectus* brain endocasts revisited. *Am J Phys Anthropol* 55:503–521.
- Howell FC. 1994. A chronostratigraphic and taxonomic framework of the origins of modern humans. In: Nitecki MH, Nitecki DV, editors. *Origins of anatomically modern humans*. New York: Plenum Press. p 253–319.
- Hublin J-J. 1978. Le torus occipital transverse et la structures associées. Evolution dans le genre *Homo*. PhD dissertation, Université de Paris VI.
- Hublin J-J. 1986. Some comments on the diagnostic features of *Homo erectus*. Fossil man, new facts—new ideas. *Anthropos* (Brno) 23:175–187.
- Jacob T. 1967. Some problems pertaining to the racial history of the Indonesian region. Utrecht: Drukkerij Neerlandia.
- Kennedy GE. 1991. On the autapomorphic traits of *Homo erectus*. *J Hum Evol* 20:375–412.
- Koengiswald GHR von, Weidenreich F. 1939. The relationship between *Pithecanthropus* and *Sinanthropus*. *Nature* 144:926–929.
- Leigh, SR. 1992. Cranial capacity evolution in *Homo erectus* and early *Homo sapiens*. *Am J Phys Anthropol* 87:1–14.
- Li T, Etler DA. 1992. New Middle Pleistocene hominid crania from Yunxian in China. *Nature* 357:404–407.
- Lumley M-A de, Sonakia A. 1985. Première découverte d'un *Homo erectus* sur le continent indien A Hathnora, dans la moyenne vallée de la Narmada. *L'Anthropologie* (Paris) 89:13–61.
- Martin R. 1914. *Lehrbuch der Anthropologie*. Jena: Gustav Fischer Verlag.
- Meindl RS, Lovejoy CO. 1985. Ectocranial suture closure: a revised method for the determination of skeletal age at death based on the lateral-anterior suture. *Am J Phys Anthropol* 68:57–66.
- Molnar S. 1972. Tooth wear and culture—a survey of tooth functions among prehistoric populations. *Curr Anthropol* 13:511–526.
- Molnar S, McKee JK, Molnar I. 1983. Measurements of tooth wear among Australian Aborigines 1: Serial loss of the enamel crown. *Am J Phys Anthropol* 61:51–65.
- Oakley KP, Campbell BG, Molleson TI. 1975. Catalogue of fossil hominids part III: Americas, Asia, Australasia. London: British Museum (Natural History).
- Openoorth WFF. 1932. *Homo (Javanthropus) soloensis*, een pleistoecene mensch van Java. *Wetesch. Mededeel. Dienst v.d. Mijnbouw in Nederl.-Indie*. 20: 49–74.
- Openoorth WFF. 1937. The place of *Homo soloensis* among fossil men. In: MacCurdy GG, editor. *Early man*. Philadelphia: J. B. Lipincott p 349–360.
- Pedersen SC, Antón SC. 1998. Bicoronal synostosis in a child from historic Omaha Cemetery 25DK10. *Am J Phys Anthropol* 105:369–376.
- Picq PG. 1990. L'articulation temporo-mandibulaire des hominides. *Cahiers de Paléanthropologie*. Paris: CNRS.
- Richards GD, Antón SC. 1991. Craniofacial configuration and postcranial development of a hydrocephalic child: with a review of cases and comment on diagnostic criteria. *Am J Phys Anthropol* 85:185–200.
- Richards LC. 1984. Principal axis analysis of dental attrition data from two Australian aboriginal populations. *Am J Phys Anthropol* 65:5–13.
- Rightmire GP. 1993. The evolution of *Homo erectus*, comparative anatomical studies of an extinct human species. New York: Cambridge University Press.
- Robinson RM, Aiello LC. 1998. A comparison of the temporal bone of aboriginal Australians with that of other modern human populations. *Am J Phys Anthropol Suppl* 26:189–190 (abstract).
- Santa Luca AP. 1980. The Ngandong fossil hominids: a comparative study of a far eastern *Homo erectus* group. *Yale University Pubs Anthro* 78:1–175.

- Simpson JS, Grün R. in press. Non-destructive gamma spectrometric U-series dating. *Quaternary Sci Rev.*
- Smith BH. 1993. The physiological age of KNM-WT 15000. In: Walker A, Leakey R, eds. *The Nariokotome Homo erectus skeleton*. Cambridge: Harvard University Press. p 195–220.
- Spitery J. 1985. Evolution de l'os frontal chez les hominidés fossiles. *L'Anthropologie (Paris)* 89:63–74.
- Stringer CB. 1984. The definition of *Homo erectus* and the existence of the species in Africa and Europe. *Courier Forschungsinstitut Senckenberg* 69:131–143.
- Swisher CC III, Rink WJ, Antón SC, Schwarcz HP, Curtis GH, Suprijo A, Widiasmoro. 1996. Latest *Homo erectus*, in Java: potential contemporaneity with *Homo sapiens* in southeast Asia. *Science* 274:1870–1874.
- Ter Haar C. 1934. *Homo soloensis*. De Ingenieur in Nederlandsch-Indie. IV. De Mijningenieur 1:51–57.
- Terra H de. 1943. Pleistocene geology and early man in Java. *Trans Am Phil Soc* 32:437–464.
- Thorne AG, Wolpoff MH. 1981. Regional continuity in Australasian pleistocene hominid evolution. *Am J Phys Anthropol* 55:337–349.
- Tobias PV. 1991. The skulls, endocasts and teeth of *Homo habilis*. *Olduvai Gorge Volume 4*. New York: Cambridge University Press.
- Tsutakawa RK, Hewett JE. 1977. Quick test for comparing two populations with bivariate data. *Biometrics* 33:215–219.
- Weidenreich F. 1940. The torus occipitalis and related structures and their transformations in the course of human evolution. *Bull Geol Soc China* 19:479–559.
- Weidenreich F. 1941. The brain and its role in the phylogenetic transformation of the human skull. *Trans Am Phil So.* 31:321–442.
- Weidenreich F. 1943. The skull of *Sinanthropus pekinensis*: a comparative study on a primitive hominid skull. *Palaeontol Sin Ser D* 10:1–298.
- Weidenreich F. 1946. *Apes, giants, and man*. Chicago: Chicago University Press.
- Weidenreich F. 1951. Morphology of Solo man. *Am Mus Nat Hist, Anthropolog Pap* 43:207–290.
- Wolpoff MH. 1996. *Human evolution*. New York: McGraw-Hill Companies, Inc.
- Wolpoff MH, Thorne AG, Jelinek J, Yinyun Z. 1994. The case for sinking *Homo erectus*. 100 years of *Pithecanthropus* is enough! In: Franzen JL, editor. *100 Years of Pithecanthropus: the Homo erectus problem*. *Courier Forschungsinstitut Senckenberg* 171:341–361.
- Wood B. 1991. *Koobi Fora Research Project, vol. 4: hominid cranial remains*. Oxford: Clarendon Press.
- Yokoyama Y, Jacob T, Falgueres C, Semah F. 1998. Direct dating of *Homo erectus* skulls of Solo man in Java by non-destructive gamma-ray. Abstracts of Dual Congress of the Intl Assoc Study Hum Paleo and Intl Assoc Hum Biol South Africa 1998:57 (abstract).